NOTES ON COLOR CHANGE AND PIGMENTARY INNERVATION IN A GOBY, A WRASSE, AND THE PLAICE

E. F. B. FRIES

(From Kristinebergs Zoologiska Station, Fiskebäckskil, Sweden, and The City College, New York)

Integumentary color change differs among teleosts. In many species it is more strictly a change of shade, while in some the hue is also actively altered. The effectors of all such changes, the chromatophores, appear to differ, according to their kind and the species in which they occur, in their mechanism of control. Recent work on teleost melanophores, going beyond the accepted conclusion that they are innervated, stresses the role of hormones (primitive, accessory, predominant, as the case may be), of double innervation in at least some species, and of chemical (neurohumoral) mediation of the nervous regulation. As for the erythrophores and xanthophores that may participate in color change, innervation seems established for some teleosts, not for others. A better unified understanding of these matters, amid so much apparent diversity, will depend on additional observation and experimentation.

To this end, exploratory study of several species of teleosts common near Fiskebäckskil [1] yielded results which, though in part incomplete or tentative, are recorded in this paper.

Methods

All the fishes were kept in running sea water, which stayed within two degrees of 17° C., and were fed every few days on minced mussels. Glass bowls, about 25 cm. in diameter, coated externally with black, white, bright rich yellow, pale blue, or vivid red paint were used to elicit the color responses. Ample daylight was admitted through large windows. All macroscopic determinations of color or adaptation were comparative, the fish being viewed simultaneously over like backgrounds, mostly white bowls or pale grayish sand. For microscopic examination of the chro-

[1] At the Kristineberg Zoological Station (of the Royal Swedish Academy of Science), on the west coast of Sweden. Accorded every facility and ready aid in supplying my wants, I owe Professor Einar Lönnberg, the director of the Station, and Dr. Gunnar Gustafson, the manager, particular acknowledgment of their hospitality.

matophores, chiefly in the tail fin, I used a dissecting binocular. Cracked ice in water served as anesthetic for the operations.

Gobius minutus Pallas

This goby ("common goby") has plentiful red and small yellow chromatophores, besides melanophores and guanin-containing elements,[2] which on the trunk are commonly joined into chromatic complexes, as detailed by Ballowitz (1913*a*, 1913*b*). In the caudal fin occur prevailingly only separate red, yellow, and black pigment cells.

Meyer (1931) has described how this fish attains, rather slowly, a color well approximating that of several experimental backgrounds. My tests of its responses to black, white, red, and yellow essentially confirmed her results as regards the rate, nature, and extent of the adaptations to these colors, except that I found, in the tail fin, poorer differentiation of xanthophore response; their pigment was not concentrated much in response to red, as compared with the dispersal evoked by yellow, and usually did not, even in nine days, become completely concentrated in response to white. Meyer did not mention blue. I found that blue evokes a response distinct from those to red and yellow (besides black and white). For example, two lots of five and four fish in two days over blue and yellow, respectively, showed macroscopic differentiation, not only slightly of shade but clearly of hue. This difference was half lost in forty-five minutes over a neutral ground of sand and reversed, as verified microscopically in the tail, in six hours over the reversed colors, yellow and blue. The blue response involves pigment concentration in both erythrophores and xanthophores, and a more nearly intermediate condition in the melanophores. Were these the only factors, there would be no difference from Meyer's results with gray; but as the skin is chromatically more complex (e.g., iridocytes and iridosomal combinations are abundant on the trunk), the goby can turn truly bluish.

Morphological color change became obvious sooner than anticipated, especially in young fish less than 4 cm. long. After five days over white, considerable degeneration of melanophores and extrusion of melanin through the epidermis (cf. Odiorne, 1936) was seen to have occurred.

In response to changed bottom color, the melanophores usually changed twice as fast as the erythrophores, yet the latter could show concentration through more than half their full range in half an hour. The more vaguely outlined xanthophores seemed slower. Meyer (1931) was impressed by the slowness of complete concentration or dispersal of the pigment, even in the melanophores, and by the relatively quick start of

[2] Compare Odiorne's (1933) description of guanophores and discussion of the terms guanophore and iridocyte.

the change, even in the erythrophores. She supplied convincing evidence of the humoral control suggested by the slowness, but did not do likewise for the direct nervous control expected on the basis of earlier work on other teleosts (e.g., von Frisch, 1911 and 1912) and indicated by the initial rapidity of the change. Unqualified reliability of the latter indication seems open to question, however, for humorally activated pigment concentration in a denervated band may occur very quickly (Fries, 1942).

More direct evidence of nervous control is supplied by denervating operations in which two or three rays of the caudal fin with their interradial tissue were severed. In gobies kept in white bowls or over pale grayish sand, such cuts, whether at the distal border of the caudal scales, or more proximally, or out in the fin, regularly provoked slow pigment dispersal in the melanophores and erythrophores, and less obviously in the xanthophores, throughout a band distal to the cut and enclosing the cut rays and their branches. The dispersal appeared first in the melanophores, evidently reached the maximum for the erythrophores in about six hours, and took a little longer in the xanthophores. Subsequently the bands tended to fade, but in the case of 3-ray bands did so only slightly, although full concentration prevailed in the intact sectors in response to a light bottom (e.g., pale sand for ten days, then white for four). In the 2-ray bands, five days over sand plus five over white sufficed for the pigment of the melanophores and erythrophores to attain typically a concentration almost equal to that evoked in the intact parts of the fin. But in fish transferred to red for five days following five over sand, the red, yellow, and black pigments were dispersed to the same extent in such 2-ray bands as elsewhere in the fin. Moreover, when white-adapted fish with almost wholly faded bands were transferred to red for several days, the band pigments became redispersed to match the chromatophores in the intact regions. The redispersal in the band erythrophores and melanophores appeared in some of the fish to lag behind the dispersal outside the band. In case of the reverse transfer from red to white of fish with the band chromatophores in the same state as in other sectors, the resulting general concentration of pigment did proceed more slowly in the band. This lagging concentration in the denervated band was clear as regards both erythrophores and melanophores, but less sure as regards the xanthophores. The lag was verified in each of three fish tested as late as nineteen days after the denervating cut. The inability of the chromatophores in the caudal bands, despite fully restored circulation, to show normal concentration in response to visual stimulation is evidence that there is direct pigment-motor innervation involving concentrating nerves. The persisting capacity for some visually-induced response is evidence of humoral control.

Signs of beginning nerve regeneration in the denervated band were noted in a few gobies examined twenty days after the nerve section. By the twenty-eighth day no lag in the responses of the band chromatophores behind the innervated chromatophores could be detected, and virtually complete regeneration was further indicated in each of three gobies in which I recut the fin through the old scar with the result that a strongly renewed full-length band was displayed in six hours by all three types of chromatophores (cf. Parker and Porter, 1933, and Abramowitz, 1935).

Thus far there is close resemblance to the chromatophores of the killifish and the catfish. It suggests that the goby's melanophores and erythrophores, if not also the xanthophores, may have the same sort of neurohumorally mediated double innervation that is strongly indicated for the melanophores of *Ameiurus*. To throw some light on this possibility, I induced the formation of three secondary caudal bands, two flanking an old primary band and the third setting off an equivalent innervated band for control, as described in an earlier report on *Fundulus* (Fries, 1942). The secondary cuts were made two weeks after the primary, which presumably allowed quite ample time for complete nerve degeneration in the primary band. More or less convincing results appeared in the 11 fish in which the three secondary bands were successfully established. In the distal portion of the primary band (flanked by the secondary bands with more extreme pigment dispersal) the melanophores and erythrophores in all 11, and the xanthophores in two or more, showed a dispersal of their pigment that was not matched in the proximal portion of the primary band and not shown at all in the control band. So stated, the effect prompts explanation in terms of Parker's hypotheses—i.e., as due to a slow diffusive spread into adjacent regions of neurohumoral material secreted by recently cut and still excited dispersing nerves in the secondary bands and to the coincident dearth of concentrating factors in the denervated primary band as compared with the innervated control band. But the pigment concentration in the primary band was not fully equal to that in the innervated regions when the secondary cuts were made; and there was already a slight tendency in several cases to less concentration throughout the distal part of the fin. Still, it seemed safe to conclude that these two possibly misleading conditions were not responsible for all the effect observed.

Accepting the results, accordingly, as having some neurohumoral significance, one may ask why they should be taken as evidence for *dispersing* neurohumors and nerves: why not regard them rather as evidence of the assumption of a resting state (dispersal) by the chromatophores when their concentrating nerves are cut and when the supply of concentrating neurohumor diffusing into old bands from regions with uncut

nerves becomes exhausted in the part of a primary band isolated by the secondary bands? Rejection of this alternative stems first from other fish where fuller work supports belief in dispersing fibers (Parker and Rosenblueth, 1941) and in a different concept of chromatophore rest (Parker, 1940*b*). I would add an observation several times verified on *Gobius*. Handling pale fish provoked rapid darkening and reddening; i.e., the innervated caudal melanophores and erythrophores showed considerable dispersal of pigment in half a minute, while band chromatophores failed to show corresponding dispersal. This phenomenon can be explained better in terms of nerves than of hormones brought from a distant gland and supplied to a week-old band as richly as to the rest of the fin. It is better ascribed to the activity of dispersing nerves (cf. Parker, 1940*c*) than to inhibition of concentrating nerves.

When making this study of *Gobius minutus,* I was unaware of Vilter's related work (1938, 1939*a,* 1939*b*). Vilter obtained certain results with *G. lota* [3] and other teleosts that he took to be in conflict with Parker's reactivation of blanched bands, viz., he was unable to get renewal of pigment dispersal in faded denervated zones by recutting (Vilter, 1938). Besides the few already mentioned tests of nerve regeneration at three and four weeks, I recut the nearly faded primary band about midway of its length in two gobies. In both of them the primary band melanophores and erythrophores distal but not proximal to the new cut showed renewed pigment dispersal. Since the recutting was done fourteen days after the original cuts (Parker, 1941, Osborn, 1939), when degeneration of the original nerve endings was supposedly complete and regeneration could hardly have begun, the results are an incentive to further tests of the non-reactivation stressed by Vilter. His negative results seem of doubtful significance until confirmed in relation to other variables (Parker, 1941), such as the extent of interference with circulation. Vilter (1938) further observed that pigment dispersal was "permanent" in the middle one of three cut rays of the dorsal fin. My observation that 3-ray caudal bands fade less than 2-ray bands is comparable. Considered with due regard for the importance of intermedin as an additional factor for pigment dispersal, both observations are in harmony with those made on bands of various widths in *Fundulus* (Parker, 1940*a*, p. 183) and hardly contradict the hypothesis of competing nerve-secreted humors. Altogether, Vilter's results as published agree with the work of Parker and others on *Fundulus* in virtually all of many particulars, with the one noteworthy exception of the non-reactivation already discussed. Vilter's explanation is clouded by his assumption that xanthophore

[3] This species seems to be the same as *G. ophiocephalus* Pallas.

change is necessarily indicative of intermedin (Vilter, 1939*b*) and not subject also to direct nervous control such as is involved in *Fundulus* (Fries, 1942) and probably in *Gobius minutus*. Thus it appears premature to reject for *Gobius* the hypothesis that its melanophores, erythrophores, and possibly xanthophores are governed by dispersing innervation in addition to concentrating nerves and pituitary secretion.

Labrus ossifagus L. (L. mixtus Krøyer)

The literature of pigmentary physiology contains, so far as my search has revealed, no account of chromatic responses in this species, though there are references (Fuchs, 1914) to other members of the genus. Younger specimens and usually the females (Lönnberg and Gustafson, 1937) of this wrasse ("striped wrasse" or "red wrasse") are richly equipped with erythrophores but comparatively sparsely with melanophores, so much so that they are more or less old-rose in general tone. Both kinds of chromatophores occur fairly uniformly throughout the caudal fin; these are of moderate size and not very elaborate form. Smaller palish xanthophores are present also, but are irregularly distributed and in the tail fin are mostly grouped in blotchy patches.

Selecting the smallest specimens of the red phase available (15–20 cm. long), I tested their adaptive responses to colored bottoms by leaving groups of two each in the different colored bowls and then making macroscopic comparison and a quick microscopic inspection of the chromatophores in the tail fin.

An initial trial showed that running water was necessary. Kept an hour or more in the bowls without change of water, six fish were pale regardless of the ground color. The pigment concentration became obvious even in the iris, contrasting with its reddish, bright appearance in all healthy fish in running water, irrespective of the color of the bowl.

With water circulation provided, a distinct difference in shade appeared as response to dark and light bottom colors. Fish from the black bowl were darkest, those from the white, palest. As the range of difference was never wide, apparently not increased in periods longer than a day, the difference between the intermediately dark fish from the red bowl and those from the black or white was not striking, but it was verified on repetition and on interchange of pairs tested. On such interchange, the naked-eye effect induced by previous shorter or longer (even 2-day) stays over the given ground color reversed itself noticeably in three minutes and virtually completely in 15 minutes. These tests of themselves permit no conclusion regarding adaptation to hue as distinguished from shade. On the other hand, the caudal chromato-

phores, in attesting the reality of the response to shade, hinted at adaptation also as concerns hue. For example, all were practically in the concentrated state, on the average not quite punctate, in fish kept for two days over a white bottom. In those equally long over black, the melanin was fully dispersed and the red pigment also dispersed but not so widely; in those over red, the erythrophores showed more dispersal of pigment (though not extreme) than the melanophores, which were at most intermediate. Thus, the erythrophores and melanophores appear to respond differentially to a red as compared to a merely dark dish. Further tests with red vs. blue and red vs. yellow showed that the fish reacted differently to each of these three colors—becoming paler and less red over blue as against red, and paler and less red (in one case more yellowish) over yellow; and also darkening when shifted to red, but not when shifted to blue, from sand—but this study was not pursued far enough to verify decisively the apparent independence of erythrophore response to hue from melanophore response to shade.

The erythrophores resembled the melanophores in the reaction to handling and holding for microscopic inspection of the tail. In fish taken from white, dispersal of both pigments past the intermediate state occurred in half a minute or less. In fish taken from black, the contrary effect, general paling, ensued also very quickly. In no changes were the erythrophores conspicuously slower than the melanophores.

Innervated chromatophores of the body in some teleosts concentrate their pigment when chilled (Smith, 1928). This labrid on immersion in iced water quickly blanched, both melanophores and erythrophores over the body evidently exhibiting more intense concentration of pigment than observed under any other circumstances; but strong dispersal followed in 10–15 minutes (still iced), in fact became so complete in one fish, which then succumbed, as to obliterate the usually persistent whitish dorsal pattern spots.

In the case of another wrasse, *Crenilabrus,* with more striking changes of hue, von Frisch (1912) has shown that the rapidly reacting erythrophores have similar nervous control to that of the melanophores. Direct innervation of both types of chromatophores also in the red wrasse is suggested by the results of cutting a brace of caudal fin rays. At first the effects were mixed, the band distal to the cut turning dark red in only one of the five and seeming even blanched in one after 15 minutes. But after a day or two, by which time circulatory deficiencies were largely ameliorated, the band was distinct in two yellow-adapted, relatively pale fish, of four surviving, and became so in the other two red-adapted fish, when transfers to blue and to white induced pigment concentration in

the erythrophores and melanophores of all intact regions, those of the denervated sector remaining in the dispersed condition. After 15 days, mostly over a sand bottom but the last nine hours over blue, the band was still distinguishable, its erythrophores in a relatively dispersed state.

This evidence warrants no conclusion regarding the exact nature of the probably nervous control of melanophores and erythrophores in this wrasse. Yet no significant difference from the functioning of the probably doubly innervated melanophores of *Fundulus* has come to light.

Pleuronectes platessa L.

These notes are based on nearly 20 young specimens, 5.5–10 cm. long, of the European plaice. These fish had abundant small melanophores, about equally numerous xanthophores, of general distribution, and a few erythrophores, which, in the fins, were irregularly scattered. The layer of close-packed "iridocytes,"[4] in which Meyer (1931) found the other chromatophores embedded, is represented even in the fins: the xanthophores are generally encircled by pale gray, opaque cells, active participants in pigmentary change, that further obscure the characteristically ill-defined xanthophores.

In a test of adaptive response to true color (denied by Schaefer, 1921, who admitted only change of shade in this species), two young plaice kept in a blue bowl for four days acquired a distinctly different coloration from two kept for the same time in a yellow bowl, the former becoming bluish gray (cf. Mast, 1916, on other flatfishes), the latter yellowish; left in white bowls, the two lots retained a noticeable difference for some hours, but lost all of it by the next day. Blanching and darkening responses to white and to black bowls were typically less slow—noticeable in half an hour—but varied according to previous history. For example, long-sustained pallor (white bowl) markedly slowed adaptive darkening (melanin dispersal). This fact implies the accumulation of a concentrating substance during white adaptation (Meyer, 1931).

The response to yellow kindled hope of obtaining evidence regarding cellular transmission of a dispersing neurohumor for comparison with that obtained from the xanthophores of *Fundulus* (Fries, 1942). But the results of cutting fin rays were uncertain, if not negative. Yellow bands due to pigment dispersal in the xanthophores were never strongly differentiated and, partly because of persistent incomplete concentration in the uncut sectors, were often not discernible at all, though they were found in several favorable instances, beginning three or four hours after the cut. These slowly reactive xanthophores seem likely to be at least

[4] Again compare Odiorne (1933) rē guanophores and iridocytes.

predominantly under humoral control like that in *Phoxinus* (Giersburg, 1932).

The same experiments did, however, yield more significant data regarding the melanophores. Caudal bands (also dorsal-fin bands) from 2-ray or 3-ray cuts in pale or intermediate plaice regularly darkened, the melanophores showing dispersal, in less than an hour, excepting that in an instance of obvious circulatory stagnation the melanophores in the band assumed a fully concentrated state. The dark bands gradually faded in pale fish, full pigment concentration taking about two weeks in 3-ray bands (cf. Osborn, 1939).[5] Faded bands redarkened more slowly than intact sectors under adaptation to black. A 19-day-old band showing this lagging dispersal (except at its proximal extremity, where nerve regeneration seemed to have begun) afforded a good demonstration also of the change progressing axipetally, as if dependent on invasions of a dispersing neurohumor—the melanophores next inside the band from the intact regions characterized by full dispersal came to show nearly full dispersal before those in the band axis changed appreciably from the concentrated state.

Out of 12 fish in which flanking and control secondary caudal bands were successfully established, five gave definite, and two others gave uncertain, indications of dispersal in the melanophores of the distal part of the faded primary band adjacent to the secondaries. A similar clear effect was elicited in just two out of the same number of equivalent operations on the dorsal fin. The mixed nature of these results recalls the case of the xanthophores of *Fundulus* (Fries, 1942).

Some sort of direct nervous control is well-attested in various other flatfishes, and Ballowitz (1893) has supplied morphological, and Schaefer (1921) physiological, evidence of it in the plaice. In so far as the spread of pigment dispersal from secondary bands into an adjoining primary band may be considered acceptable evidence of the existence of dispersing nerves and their neurohumor in *Fundulus,* one may conclude—without prejudice to the possibilities of supplementary influence by an adrenaline-like factor in the blood (Osborn, 1939), by the pituitary hormone (cf. E. Meyer, 1931, Osborn, 1939, H. H. Meyer, 1939*a*), or by a retinal substance reported by Meyer (1939*b*) to cause paling in the plaice—that my results with the plaice point to similar dual nervous control for the melanophores in this species.

[5] As of interest in relation to the very long-maintained darkening of wide denervated bands observed by Osborn in *Pseudopleuronectes americanus,* it may be stated that 3-ray caudal bands in four *Pleuronectes flesus* (about 15 cm. long) failed to pale, except irregularly and along their margins, to match the pale innervated areas in the 26 days that I kept these flounders (over a gray-white bottom).

Summary

Colored bowls evoked characteristic chromatophore responses in *Gobius minutus, Labrus ossifagus,* and *Pleuronectes platessa.* The responses, including those to blue and to yellow, effected differential adaptation of integumentary hue as well as shade, especially in the goby and the plaice. They confirmed that erythrophores, xanthophores, and melanophores may act independently, pigment dispersal in erythrophores and xanthophores depending on the color of the bottom while melanophores respond according to its darkness.

The changed chromatophore behavior resulting from fin cuts producing denervated bands indicated that the melanophores, erythrophores, and perhaps the xanthophores are innervated at least by concentrating fibers in the goby and that the erythrophores and melanophores are probably innervated in the wrasse.

Denervation experiments supplied evidence consistent with the hypothesis that dispersing as well as concentrating nerves and their neurohumors control the goby's melanophores and erythrophores and the plaice's melanophores. This evidence includes renewed pigment dispersal in the distal part of a faded, primary band where flanked by new, secondary bands (goby and plaice) and rapid dispersal in the not denervated melanophores and erythrophores when the fish were handled (goby).

LITERATURE CITED

Abramowitz, A. A., 1935. Regeneration of chromatophore nerves. *Proc. Nat. Acad. Sci.,* **21**: 137–141.

Ballowitz, E., 1893. Die nervenendigungen der Pigmentzellen, ein Beitrag zur Kenntnis der Zusammenhang der Endverzweigungen der Nerven mit dem Protoplasma der Zellen. *Zeitschr. wiss. Zool.,* **56**: 673–706.

——, 1913*a*. Über schwarzrote Doppelzellen und andere eigenartige Vereinigungen heterochromer Farbstoffzellen bei Knochenfischen. *Anat. Anz.,* **44**: 81–91.

——, 1913*b*. Über schwarzrote und sternförmige Farbzellenkombinationen in der Haut ven Gobiiden. Ein weiterer Beitrag zur Kenntnis der Chromatophoren und Chromatophoren-Vereinigungen bei Knochenfischen. *Zeitschr. wiss. Zool.,* **106**: 527–593.

Fries, E. F. B., 1942. Some neurohumoral evidence for double innervation of xanthophores in killifish (Fundulus). *Biol. Bull.,* this issue.

Frisch, K. von, 1911. Beiträge zur Physiologie der Pigmentzellen in der Fischhaut. *Arch. ges. Physiol.,* **138**: 319–387.

——, 1912. Ueber farbige Anpassung bei Fischen. *Zool. Jahrb., Abt. allg. Zool. Physiol.,* **32**: 171–230.

Fuchs, R. F., 1914. Der Farbenwechsel und die chromatische Hautfunktion der Tiere. Winterstein, Handbuch vergl. Physiol., Bd. 3, H. 1, T. 2: 1189–1656.

Giersberg, H., 1932. Der Einfluss der Hypophyse auf die farbigen Chromatophoren der Elritze. *Zeitschr. vergl. Physiol.,* **18**: 369–377.

Lönnberg, E., and G. Gustafson, 1937. Contribution to the life-history of the striped wrasse, Labrus ossifagus Lin. *Ark. Zool.,* **29A**: No. 7, 1–16.

MAST, S. O., 1916. Changes in shade, color, and pattern in fishes, and their bearing on the problems of adaptation and behavior, with especial reference to the flounders Paralichthys and Ancylopsetta. *Bull. U. S. Bur. Fish.*, **34**: 173–328.

MEYER, EVA, 1931. Versuche über den Farbwechsel von Gobius und Pleuronectes. *Zool. Jahrb., Abt. allg. Zool. Physiol.*, **49**: 231–270.

MEYER, H. H., 1939*a*. Der Nachweis von Melanophorenhormon in der Hypophyse der Fische. *Endokrin.*, **22**: 137–144.

——, 1939*b*. Über ein Hormon der Fisch Retina. *Endokrin.*, **22**: 261–279.

ODIORNE, J. M., 1933. The occurrence of guanophores in Fundulus. *Proc. Nat. Acad. Sci.*, **19**: 750–754.

——, 1936. The degeneration of melanophores in Fundulus. *Jour. Exp. Zoöl.*, **74**: 7–39.

OSBORN, C. M., 1939. The physiology of color change in flatfishes. *Jour. Exp. Zoöl.*, **81**: 479–515.

PARKER, G. H., 1940*a*. Neurohumors as chromatophore activators. *Proc. Amer. Acad. Arts Sci.*, **73**: 165–195.

——, 1940*b*. The active and the resting states of catfish melanophores tested experimentally. *Jour. Cell. Comp. Physiol.*, **15**: 137–146.

——, 1940*c*. On the neurohumors of the color changes in catfishes and on fats and oils as protective agents for such substances. *Proc. Amer. Phil. Soc.*, **83**: 379–406.

——, 1941. Melanophore bands and areas due to nerve cutting, in relation to the protracted activity of nerves. *Jour. Gen. Physiol.*, **24**: 483–505.

PARKER, G. H., AND H. PORTER, 1933. Regeneration of chromatophore nerves. *Jour. Exp. Zoöl.*, **66**: 303–309.

PARKER, G. H., AND A. ROSENBLUETH, 1941. The electric stimulation of the concentrating (adrenergic) and the dispersing (cholinergic) nerve fibers of the melanophores in the catfish. *Proc. Nat. Acad. Sci.*, **27**: 198–204.

SCHAEFER, J. G., 1921. Beiträge zur Physiologie des Farbenwechsels der Fische. I. Untersuchungen an Pleuronectiden. II. Weitere Untersuchungen. *Arch. ges. Physiol.*, **188**: 25–48.

SMITH, D. C., 1928. The effect of temperature on the melanophores of fishes. *Jour. Exp. Zoöl.*, **52**: 183–233.

VILTER, V., 1938. Déterminisme mélano-contricteur de bandes d'assombrissement consécutives au sections nerveuses dans la nageoire dorsale de Gobius. *C. R. Soc. Biol.*, **129**: 1166–1168.

——, 1939*a*. Configuration des dermatomes pigment-moteurs chez les Téléstéens et modalités de leur recouvrement réciproque. *C. R. Soc. Biol.*, **130**: 388–390.

——, 1939*b*. Évolution des bandes sombres provoquées par la section de nerfs pigment-moteurs chez les Téléostéens. Intervention de la circulation en tant que vecteur des hormones pigmentomotrices. *C. R. Soc. Biol.*, **130**: 391–394.